NESTING ECOLOGY OF MIGRATORY GOLDEN EAGLES (*Aquila chrysaetos*) IN DENALI NATIONAL PARK, ALASKA

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A

Thesis

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ABSTRACT

Between 1988 and 1993 I measured occupancy of nesting territories and reproduction of golden eagles (*Aquila chrysaetos*) in Denali National Park, Alaska. I collected data occupancy of nesting territories and three reproductive variables (pairs nesting, pairs producing fledglings, and fledgling production) at 74 nesting territories using three aerial surveys each year. During my study, annual fledgling production varied nearly threefold, from 20 fledglings in 1992 to 58 fledglings in 1989. Although rates of nesting territory occupancy did not vary significantly among years ($\chi^2 = 8.21$, d.f. = 5, $P = 0.114$), I noted significant variation in the proportion of pairs laying eggs ($\chi^2 = 33.12$, d.f. = 5, $P < 0.001$) and the proportion of pairs fledging young ($\chi^2 = 16.03$, d.f. = 5, $P = 0.007$) among years. Decreases in pairs laying eggs were correlated with decreases in average daily numbers of snowshoe hare (*Lepus americanus*) and willow ptarmigan (*Lagopus lagopus*) observed in the study area ($r_s = 0.83$, $P = 0.04$).

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This thesis is dedicated to John Dalle-Molle. May his spirit always soar over the wilds of Alaska.

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INTRODUCTION

Golden eagles (*Aquila chrysaetos*) are one of most widespread species of eagle in the world (Brown and Amadon 1968, Cramp and Simmons 1980, Palmer 1988). They are also one of the more widely studied *Aquila* species (see LeFranc and Clark 1983). In the western palearctic, many studies have been conducted on nesting ecology of golden eagles (Watson 1957, Brown and Watson 1964, Lockie and Ratcliffe 1964, Brown and Amadon 1968, Cramp and Simmons 1980, Michel 1986, Bahat 1989, Watson et al. 1992) including several studies made at higher latitudes in Sweden (Tjernberg 1981, Tjernberg 1983a, Tjernberg 1983b), Norway (Bergo 1984a, Bergo 1984b, Bergo 1987, Gjershaug *In press*), and Finland (Sulkava 1984). In North America, many studies have been conducted on ecology of golden eagles (Murie 1944, Spofford 1964, McGahan 1966, McGahan 1968, Spofford 1971, Kochert 1972, Collopy 1980, Palmer 1988, Lehman et al. 1993). Few ecological studies of golden eagles, however, have been conducted in the northern regions of North America.

Although golden eagles are widely distributed in Alaska and northwestern Canada (Palmer 1988), little is known about reproduction of the species near the northern limit of its breeding distribution in North America (but see Mossop et al. 1986, Poole and Bromley 1988, Kessel 1989, Morneau et al. 1994, Young et al. 1995). In Alaska, most information on golden eagles is from short-term studies, is based on small sample sizes, or has been collected concurrently withother studies (Murie 1944, White 1974, Swartz et al. 1975, White et al. 1977, Ritchie and Curatolo 1982, Kessel 1989, Petersen et al. 1991, Young et al. 1995). Although this information is valuable, comprehensive, long-term studies on golden eagles are essential to form clearer pictures of their life-history traits in the subarctic and Arctic.

Throughout their range, most studies of golden eagles have been conducted in areas where golden eagles are residents on their nesting territories. Most golden eagles from northern and interior Alaska, however, are migratory (Gabrielson and Lincoln 1959) and their migration and wintering periods may occupy more than 5 months each year. This life history is typical for many birds breeding in the subarctic and Arctic (Ens et al. 1990) and entails high-energy demands for migration immediately before reproduction. Consequently, reproductive strategies of migratory golden eagles in subarctic ecosystems could be considerably different from those of resident golden eagles in other geographic areas.

Between 1987 and 1995 I studied several aspects of nesting ecology of golden eagles in Denali National Park and Preserve (hereafter "Denali") in central Alaska. Between 1988 and 1993, I monitored 74 golden eagle nesting territories for six consecutive breeding seasons to document population status and describe reproductive characteristics of golden eagles. Each year I documented the number of territories occupied by pairs of eagles and collected data on number of pairs with eggs, number of pairs with fledglings, and number of fledglings produced. Because detailed demographic data (e.g., survivorship, longevity, recruitment rates, age structure, and sex structure) are not available for golden eagles, I used occupancy and reproductive data to make inferences about the status of the local population (following Steenhof and Kochert 1982, Steenhof 1987).

In this thesis I: (1) document annual nesting territory occupancy rates; (2) describe and quantify variation in three reproductive variables (pairs nesting, pairs successful, and fledgling production); (3) describe nesting phenology; (4) compare reproductive characteristics of golden eagles in Denali to those of golden eagles in other geographic study areas; (5) evaluate relationships between reproduction and environmental factors (e.g., weather and selected food supplies) that could cause variation in reproduction in golden eagles; (6) make inferences about the status of the local population of golden eagles breeding in Denali; and (7) make suggestions about factors that may influence golden eagle reproduction in Denali.

STUDY AREA

The 2,500 km^2 study area (centered at 63° 35'N, 149° 30'W) lies on the north side of the Alaska Range in central Alaska, within the northeastern portion of Denali National Park and Preserve (Fig. 1). Terrain in the area is mountainous with a combination of rugged ridge tops, rounded summits, precipitous cliff faces, and talus slopes. The mountains are interspersed by broad glacial river valleys, low rolling

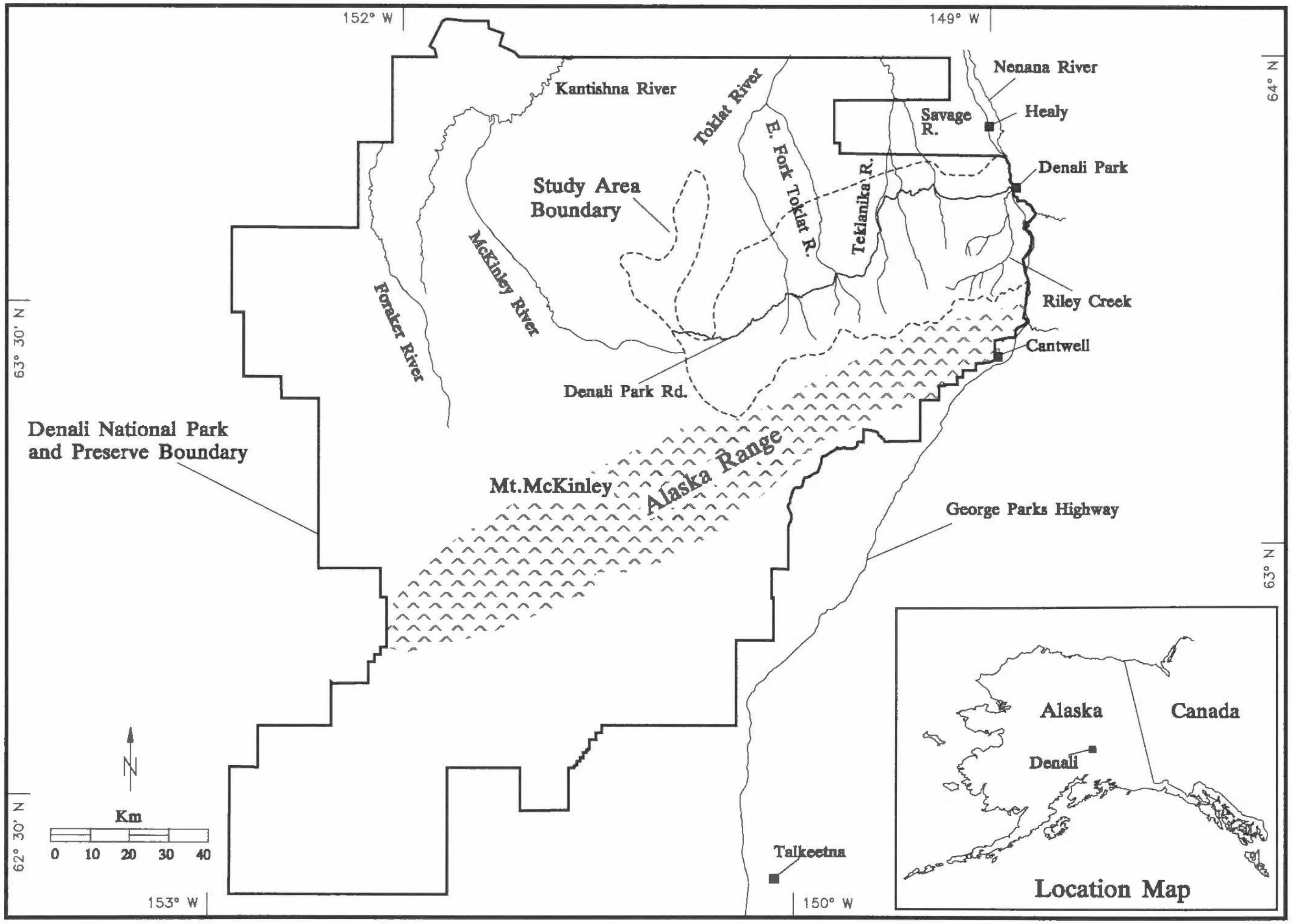


Figure 1. Study area (shaded region) in Denali National Park and Preserve, Alaska.

tundra, and upland areas. Elevations in the study area range from 350 m along rivers to 2,000 m just north of the crest of the Alaska Range.

Most of the study area lies above tree line, which occurs at 800 m. Vegetation in the area include lichens covering the thin alpine soil and talus slopes, narrow forest stands along rivers and streams, and a mixture of herbaceous shrubs, flowering plants, and grasses. Sheldon (1930), Dixon (1938) and Murie (1944, 1963, 1983) provide detailed descriptions of the vegetation in the area.

The climate is cold and dry with long, cold winters and short, cool summers. Snow and ice permanently cover areas above 2,500 m. From 1988 through 1993, snow cover persisted at lower elevations from mid-September through mid-May, a period of 210 days, on average (NPS, unpublished data).

A variety of mammals and birds, many that are commonly eaten by golden eagles (Murie 1944, McIntyre, unpublished data), occur in the study area. Three species of ptarmigan, willow (*Lagopus lagopus*), rock (*L. mutus*), and white-tailed (*L. leucurus*), occur in the study area; the willow ptarmigan is the most common and widely distributed species (Dixon 1938, Murie 1963). Murie (1983) described five species of shrews and seven species of voles in the region. Snowshoe hare (*Lepus americanus*) inhabit the timbered portions of the study area and willow (*Salix* spp.) thickets above and below treeline. Hoary marmot *(Marmota caligata*) occur at higher elevations. Arctic ground squirrel (*Spermophilus parryii*) are abundant throughout the study area.

Larger mammals, including coyote (*Canis latrans*), wolf (*C. lupus*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), brown bear (*Ursus arctos*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall's sheep (*Ovis dalli*), also occur in the study area.

Between 1987 and 1993, Arctic ground squirrel, snowshoe hare, willow ptarmigan, and hoary marmot were the most common species brought to nests by nesting golden eagles (McIntyre, unpublished data) in Denali. Although willow ptarmigan and snowshoe hare are available as food throughout the nesting season, annual numbers of snowshoe hare and willow ptarmigan fluctuate between periodic lows and highs in the area (Dixon 1938). Arctic ground squirrels usually emerge from hibernation in mid- to late-April (Dixon 1938), after most golden eagles lay eggs. Murie (1983) reported no indication of population cycles in ground squirrels in Denali.

Most of the study area is within a federally designated Wilderness Area and an internationally recognized Biosphere Reserve. The heaviest human visitation occurs in summer and concentrates primarily along the seasonal road that traverses the study area.

METHODS

Since 1908, locations of golden eagle nests in Denali have been recorded by many researchers and park personnel (McIntyre et al. 1988). Intensive surveys of golden eagle were initiated in the study area in 1987 (Britten and McIntyre 1988). As of 1993 I had delineated 100 different nesting territories of golden eagles. My analyses in this study, however, are based on data collected at 74 territories (Fig. 2) where complete surveys were conducted each year between 1988 through 1993.

Definitions

Terminology describing nesting activity follows Postupalsky (1983), Newton and Marquiss (1982), Steenhof (1987) and R. Ambrose (pers. comm.). I defined a nesting territory as an area containing one or more nest structures that belonged to one pair of eagles in a year. Using the history of nest use and location of nest structures (e.g., distance from other nests or groups of nests), I grouped nest structures into nesting territories. I considered a nesting territory occupied if I located a territorial pair or evidence of a territorial pair (e.g., incubating bird, nest construction or nest maintenance). If criteria for occupation were not met after at least 4 hrs of continuous observation during the incubation period, I defined a nesting territory as unoccupied. If criteria for occupation were not met, but observations were made for < 4 hrs during the incubation period, I defined a nesting territory as presumed unoccupied. I defined a territorial pair of eagles with eggs as a nesting pair. Because I did not flush eagles off nests to count eggs, I presumed that birds observed in incubating postures had eggs. Chicks < 51 days old were called nestlings. For data analysis, I considered nestlings that reached 51 days-of-age (or 80% of the mean age at first flight) as

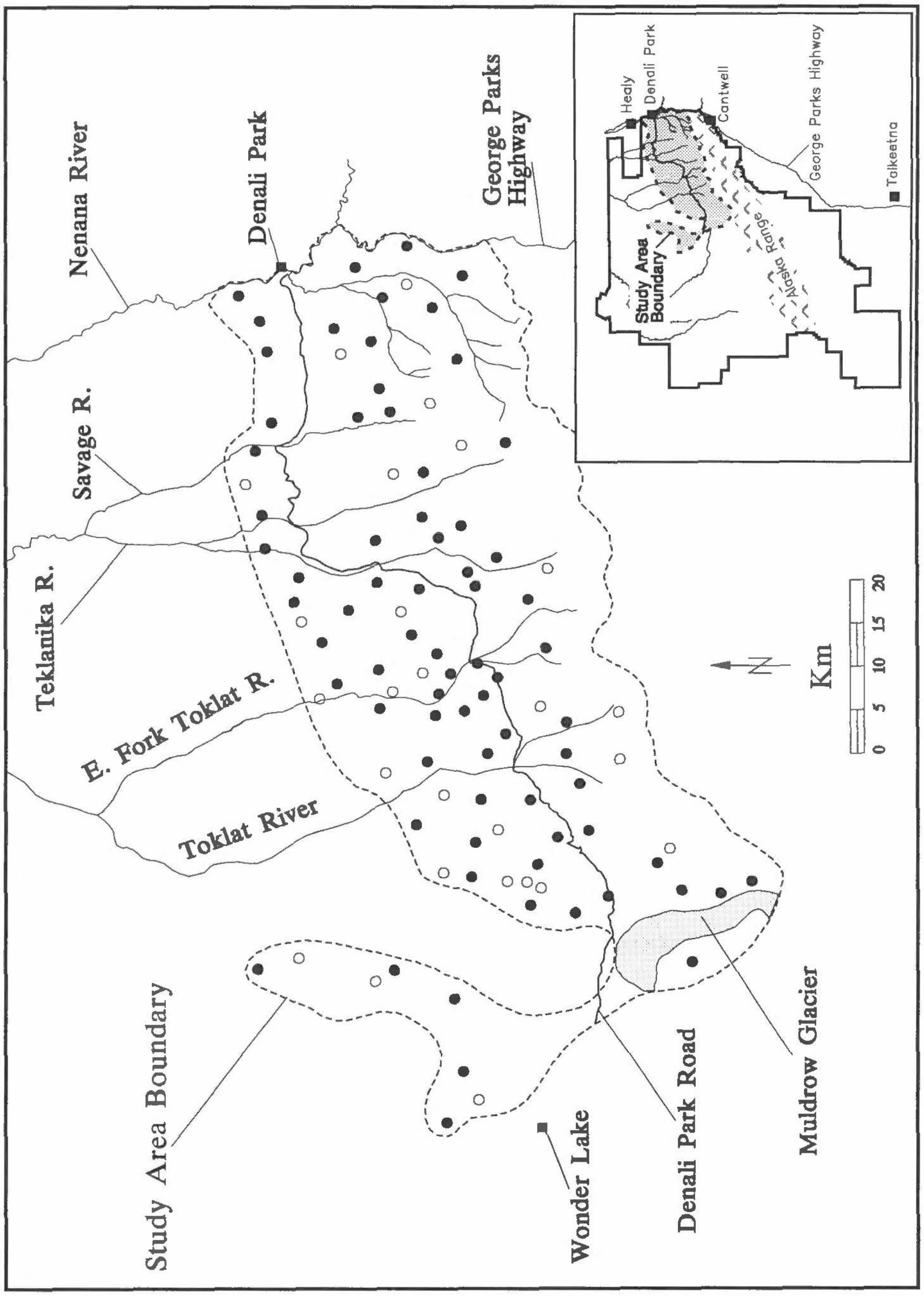


Figure 2. Location of nesting territories, Denali National Park, Alaska. Solid circles represent nesting territories where data were collected over 6 consecutive years, 1988-1993.

fledglings (Steenhof 1987). These criteria were used because making observations of all nests on exact fledging dates was impossible, and nestling mortality after 51 days of age but before actual fledging was usually minimal (Millsap 1981, Steenhof 1987). A territorial pair that produced ≥ one fledgling was considered a successful pair. I defined nesting success as the percentage of territorial pairs that produced ≥ 1 fledgling. I defined productivity as the number of fledglings produced per territorial pair. For comparative purposes and to provide insights into the stage of the nesting cycle in which failures may have occurred, I also report mean number of fledglings per nesting pair and per successful pair.

I based my estimates of productivity on territorial pairs for several reasons. First, ideally, reproductive statistics should be reported per breeding-age female (Steenhof 1987), however, I could not enumerate the nonterritorial segment of the local population. Second, because pairs of golden eagles do not lay eggs every year, excluding nonbreeding pairs from my analyses would be incorrect and misleading (Steenhof 1987). Finally, by themselves, estimates of numbers of fledglings produced per breeding pair or per successful pair can be misleading because successful pairs often produce normal numbers of fledglings even during periods of depressed productivity of the population (Brown 1974, Steenhof 1987).

Surveys

I collected data on nesting territory occupancy and reproduction using three aerial surveys each year. Timing of the first survey in 1988 was based on data on nesting phenology collected in the study area in 1987 (Britten and McIntyre 1988). In all years the first annual survey was conducted on 2 - 4 consecutive days in late April-early May to document occupancy and nesting activity at nesting territories. At this time, most clutches were completed, but hatching had not occurred. Nesting territories classified as presumed unoccupied during this survey were revisited later during incubation. The second survey was flown on 1day in late June to count nestlings at territories where I noted nesting pairs during the first annual survey. By this time most young were > 21 days old. The final annual survey was conducted on 1 day in late July or early August to count fledglings at territories where nestlings had been observed during the second survey. By the time of this survey most nestlings were ≥ 51 days old, but few had fledged.

All aerial surveys were conducted using a Bell 206B Jet Ranger helicopter. During the incubation surveys I was assisted by one experienced observer who sat directly behind me. For all other surveys I was helped by one or two experienced observers. During all surveys the helicopter was flown at 30-40 km/hr and periodically at hover while observing nest contents. A minimum distance of at ≥ 100 m between the helicopter and nest structures was maintained during all aerial surveys. When I could not determine occupancy or nesting activities from the helicopter, the helicopter landed and I made observations from vantage points on the ground. I used binoculars

(8 X 30) during all aerial surveys and a spotting scope (15-45) during ground observations. During all field activities I followed recommendations made by Fyfe and Olendorff (1976) to avoid disturbing adults and nestlings.

Nesting Phenology

I visited selected nests to band nestlings and collect prey remains following the second annual survey each year. My estimates of annual nesting phenology of golden eagles in Denali were based on estimates of nestling ages made during visits to nests. To calculate annual phenology of nesting seasons in Denali, I made the following assumptions: incubation began with the first egg (Palmer 1988), the incubation period was 45 days (Palmer 1988), and fledging occurred after chicks were 64 days-of-age (Steenhof 1987). I calculated dates of hatching by backdating from estimated age of nestlings; age of nestlings was estimated using morphological measurements and a photographic key for aging (Hoechlin 1976). Dates of laying were estimated by subtracting 45 days from estimated dates of hatching.

Trends in food supply

To detect broad-scale trends on the populations of snowshoe hare and willow ptarmigan, I recorded numbers of each species seen during routine field activities each day (following Kochert 1980). Kochert (1980) reported that estimates of black-tailed jackrabbits (*L. californicus*) made from counts during his routine field activities provided results comparable to estimates made from flushing transects.

All counts of hares were made from the ground, while ptarmigan were counted during aerial surveys and from the ground. Mean numbers of hare and ptarmigan observed each day were tabulated from field notes. Because I visited the same areas and devoted similar effort to counting hare and ptarmigan each year, I assumed that my counts were comparable among years and that they provided data for detecting broad trends of annual hare and ptarmigan numbers.

To detect relationships between food and golden eagle reproduction, I constructed an index of relative abundance of food (food index) using a combined count of hare and ptarmigan. The index was constructed by adding the counts of hare and ptarmigan observed each year and dividing by two. To obtain equal sample sizes each year, count data were randomly selected until 26 count days (the minimum number of count days in 1992) were selected each year.

Trends in weather

For analyses I used weather data (mean maximum daily temperature, mean minimum daily temperature, total precipitation, and number of days with precipitation) collected at the Denali National Park and Preserve headquarters by National Park Service staff. Numbers of nesting pairs were compared with weather variables collected from 15 March to 15 April, or from about 3 weeks before laying to the initiation of laying. I chose this period because weather during this period should have had the greatest effect on laying (Newton 1986). I compared nesting success and productivity with weather variables collected from 16 April to 30 June, or from laying through the early nestling stage. I chose this period because weather during this period should have had the greatest effect on incubation, energy requirements, and hunting efficiency of nesting pairs and nestlings.

Statistical analysis

I used a two-way analysis of variance (ANOVA) to detect variation in productivity among years. Tukey's multiple comparison procedure (Tukey's test) was used to assess the statistical significance of differences in productivity.

I used the Kruskal-Wallis test to detect annual variation in: (1) mean number of snowshoe hare observed per day; (2) mean number of willow ptarmigan observed per day; (3) annual values for the food index; (4) mean annual dates of hatching; and (5) annual mean measurements of weather variables. Nonparametric multiple comparison tests for Kruskal-Wallis were used to identify which differences among groups accounted for the significant overall F-value.

Chi-square analyses were used to detect annual variation in nesting territory occupancy, pairs nesting, nesting success and brood sizes. Multiple comparisons for proportions were used to detect which annual proportions were different from others for Chi-square analyses.

I used Spearman rank correlations (r_s) to examine associations between: (1) food index values and pairs nesting; (2) food index values and nesting success; (3) food index values and productivity; (4) weather variables and reproduction; and (5) weather variables and nesting phenology. I used linear regression to examine relationships hatching dates and mean brood size at fledging. To control for variation in nesting phenology among years, I coded 155 hatching dates by determining the difference in actual hatch date and mean hatch date for that year.

Differences among years and relationships between variables were considered significant when $\underline{P} < 0.05$. Statistical analyses followed Sokal and Rohlf (1981) and Conover (1980). Statistical analyses were conducted using BMDP (Dixon 1992) and STATISTIX© (Analytical Software 1985) statistical software.

RESULTS

Reproduction

During my six-year study, the number of fledglings produced annually varied nearly threefold, from 20 in 1992 to 58 in 1989 (Table 1; Appendix 1). Occupancy of nesting territories rates averaged 74.3% (Table 1) and did not vary significantly among years ($\chi^2 = 8.21$, d.f. = 5, $P = 0.144$). I noted significant variation in the proportion of territorial pairs laying eggs among years ($\chi^2 = 33.12$, d.f. = 5, $P < 0.001$; Table 1), and the proportion of pairs producing fledglings among years ($\chi^2 = 16.03$, d.f. = 5, $P = 0.007$; Table 1). Fewer pairs laid eggs and raised fledglings in 1992 and 1993 than in all other years (multiple comparisons test for proportions, $P = 0.009$ and $P < 0.001$,

Table 1. Summary of nesting territory occupancy and reproductive characteristics of golden eagles, Denali National Park, Alaska, 1988-1993. Data were collected at 74 nesting territories over six consecutive years.

Year	Occupied territories (%)	Nesting pairs (%)	Successful pairs (%)	Total fledglings	Fledglings/ occupied territory	Fledglings/ nesting pair	Fledglings/ successful pair
1988	61 (82.4)	47 (77.0)	36 (59.0)	52	0.85	1.11	1.44
1989	52 (70.3)	45 (86.5)	34 (65.4)	58	1.12	1.29	1.71
1990	49 (66.2)	40 (81.6)	29 (59.2)	46	0.94	1.15	1.58
1991	52 (70.3)	39 (75.0)	33 (63.5)	51	0.98	1.31	1.55
1992	56 (75.7)	33 (58.9)	15 (26.8)	20	0.36	0.61	1.33
1993	60 (81.1)	27 (45.0)	17 (28.3)	24	0.40	0.89	1.41
Mean	55.0 (74.3)	38.5 (70.7)	27.3 (50.4)	41.8	0.78	1.06	1.50
S.D.	4.8	7.5	9.1	15.9	0.32	0.27	0.14

respectively). Productivity differed significantly among years ($F = 7.45$, d.f. = 5,67, $P < 0.001$); productivity was lower in 1992 and 1993 than in all other years (Tukey's test, $P < 0.001$).

Broods with a single fledgling were more common than larger broods (Table 2). Distribution of brood sizes, however, did not vary among years ($\chi^2 = 9.62$, d.f. = 10, $P = 0.475$). Of 231 nesting attempts I observed, 67 resulted in failure. Most failures (82.1%) occurred before nestlings reached 21 days-of-age. Although causes of individual nest failures were unknown, I did not document nest predation.

Nesting phenology

On average, hatching began on 27 May (SD = 7.2 days, n = 6 years) and ranged from 8 May to 16 June (Table 3). Spread in hatching dates ranged from 14 days in 1993 to 36 days in 1989. Mean hatching dates differed significantly among years ($H = 38.53$, $P < 0.001$: Fig. 3). Mean hatching dates were earlier in 1990 and 1991 than other years (multiple comparisons test, $P < 0.001$).

I failed to detect any relationships between hatching dates and weather variables measured from 15 March - 15 April annually. Likewise, I failed to detect relationships between mean hatching date and mean brood size at fledgling ($F = 1.01$, d.f. = 154, $P = 0.39$). Relationships between laying dates and nesting success could not be examined because estimates of nesting phenology were based on successful nests, and laying dates for all clutches were not known.

Table 2. Brood-sizes of successful pairs of golden eagles, Denali National Park, Alaska, 1988-1993.

Year	Brood-size		
	One fledgling (%)	Two fledglings (%)	Three fledglings (%)
1988	20 (55.6)	16 (44.4)	0
1989	14 (41.2)	16 (47.1)	4 (11.8)
1990	14 (48.3)	13 (44.8)	2 (6.9)
1991	18 (54.6)	12 (36.3)	3 (9.1)
1992	10 (66.7)	5 (33.3)	0
1993	10 (58.8)	7 (41.2)	0
Total and Mean %	86 (52.4)	69 (42.1)	9 (5.5)

Table 3. Estimated dates of egg laying and hatching for golden eagles, Denali National Park, Alaska, 1988-1993. Hatching dates were estimated by backdating from estimated ages of nestlings at successful nests. Laying dates were estimated by subtracting 45 days from median and mean hatch dates.

Year	Estimated laying dates		Estimated hatching dates		SD[a] (days)	n
	Median	Mean	Median	Mean		
1988	12 April	13 April	27 May	28 May	6.19	37
1989	17 April	16 April	1 June	31 May	8.24	37
1990	4 April	6 April	19 May	21 May	6.84	29
1991	7 April	9 April	22 May	24 May	5.90	28
1992	13 April	12 April	28 May	27 May	4.94	17
1993	14 April	13 April	29 May	28 May	4.34	22

[a] SD = Standard deviation

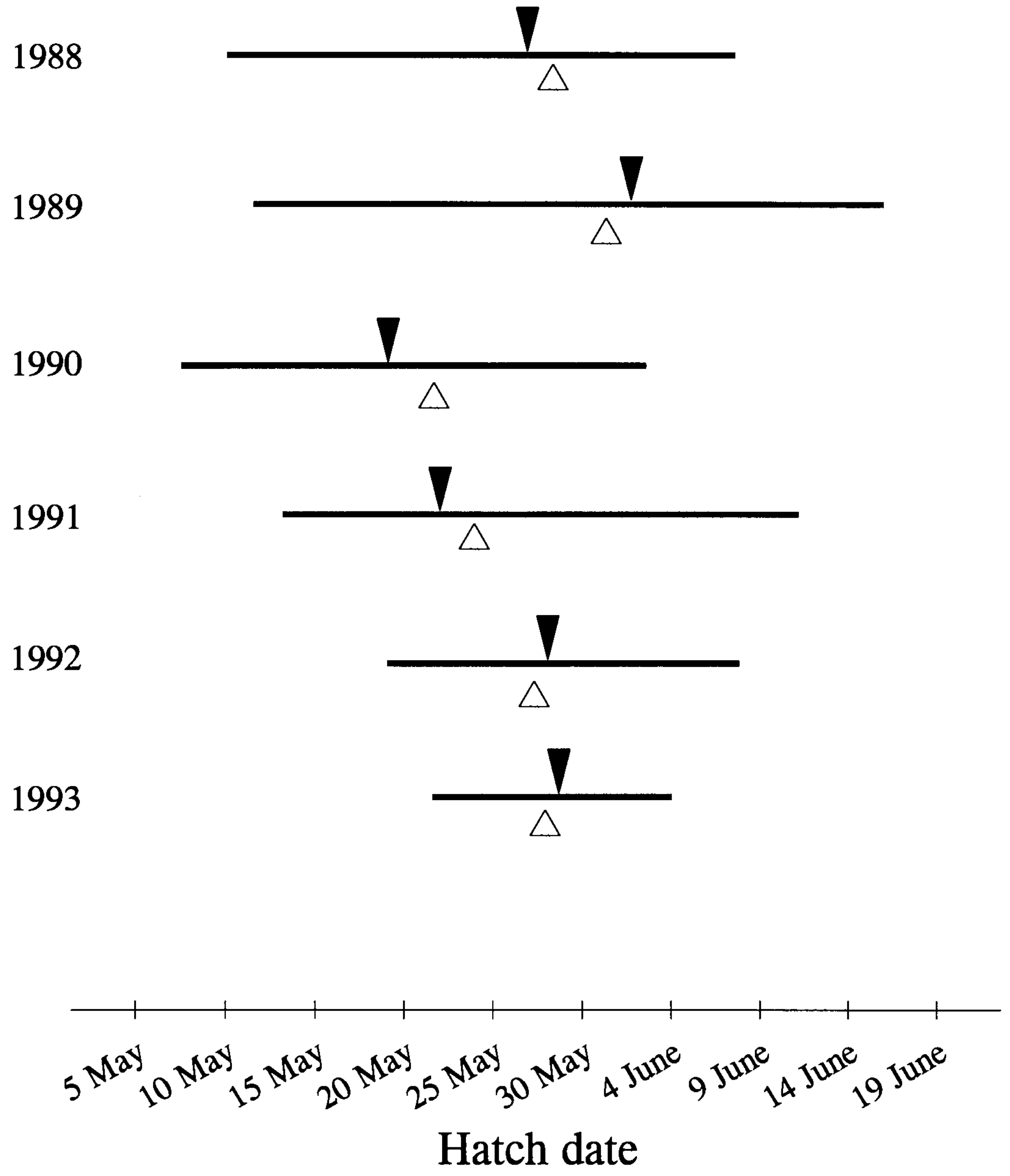


Figure 3. Estimated hatching dates for golden eagles, Denali National Park, Alaska, 1988-1993. Horizontal lines represent range of hatch dates for each year. Solid arrows above lines denote median hatching date each year. Open arrows below lines denote mean dates of hatching.

Food and golden eagle reproduction

The mean annual numbers of snowshoe hare and willow ptarmigan I counted exhibited parallel downward trends (Fig. 4) and differed significantly among years ($H = 182.43$, $P < 0.001$ for hare, $H = 179.42$, $P < 0.001$ for ptarmigan).

Food-index values declined significantly from 1988 to 1993 ($H = 126.71$, $P < 0.001$) and I detected a significant relationship between percentage of pairs nesting and these values ($r_s = 0.83$, $P = 0.04$; Fig. 5). The trend in Fig. 5, however, suggests a threshold may exist beyond which increased food supply does not influence laying. I failed to detect relationship between nesting success and the food index ($r_s = 0.45$, $P = 0.34$), or productivity and the food index ($r_s = 0.54$, $P = 0.26$).

Weather and reproduction

Mean maximum daily temperature, mean minimum daily temperature and total precipitation varied markedly among years (Figs. 6 and 7). Weather in May 1992 was particularly severe, with record snowfall (623 mm) and below average temperatures. Total snowfall in May 1992 (623 mm) was five times greater than May snowfall in all other years combined (120 mm). Spring 1993 was warm and dry, with < 2 mm of precipitation recorded from March - May. I failed to detect a relationship between weather variables and reproduction variables (Table 4). Statistical power of these tests, however, was low because only 6 years of data were available for analysis.

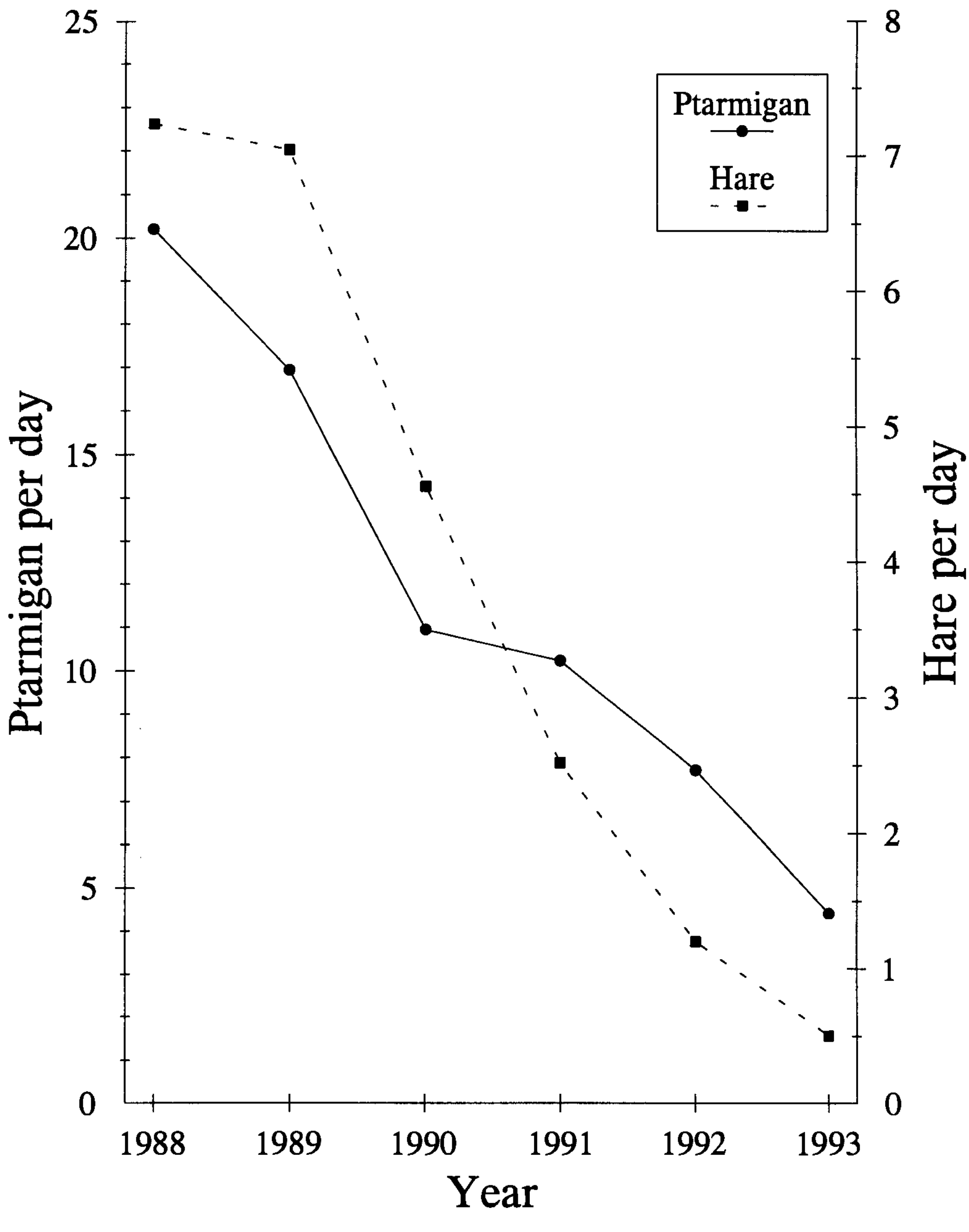


Figure 4. Trends in annual mean number of willow ptarmigan (*Lagopus lagopus*) and snowshoe hare (*Lepus americanus*) observed in study area, Denali National Park, Alaska, 1988-1993.

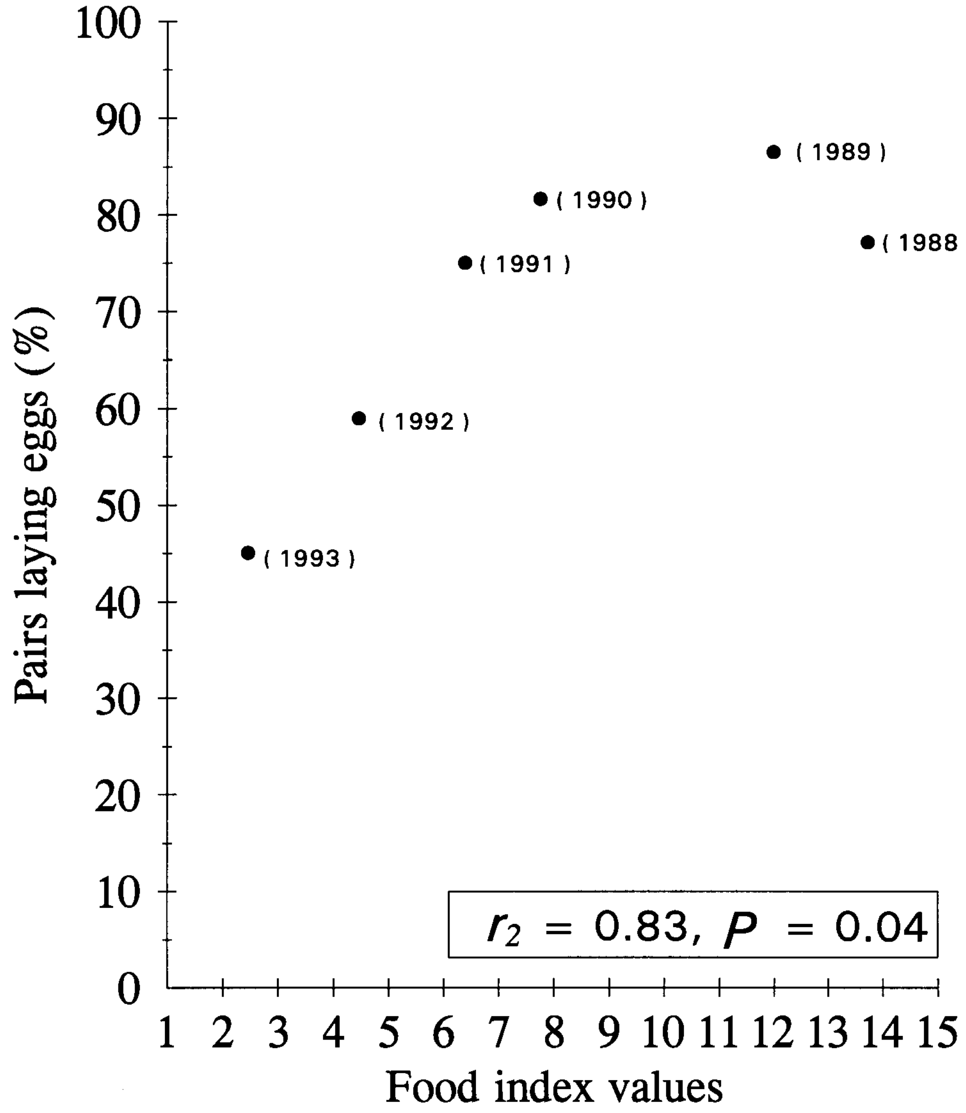
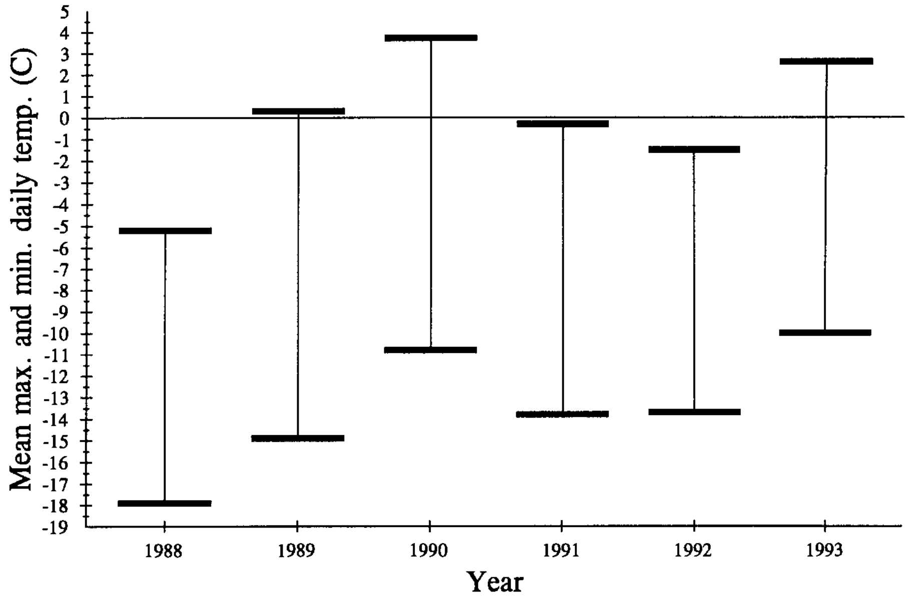


Figure 5. Correlation between pairs of golden eagles laying eggs (%) and food index values, Denali National Park, Alaska, 1988-1993. Food index values are calculated from annual counts of willow ptarmigan (*Lagopus lagopus*) and snowshoe hare (*Lepus americanus*) in the study area.



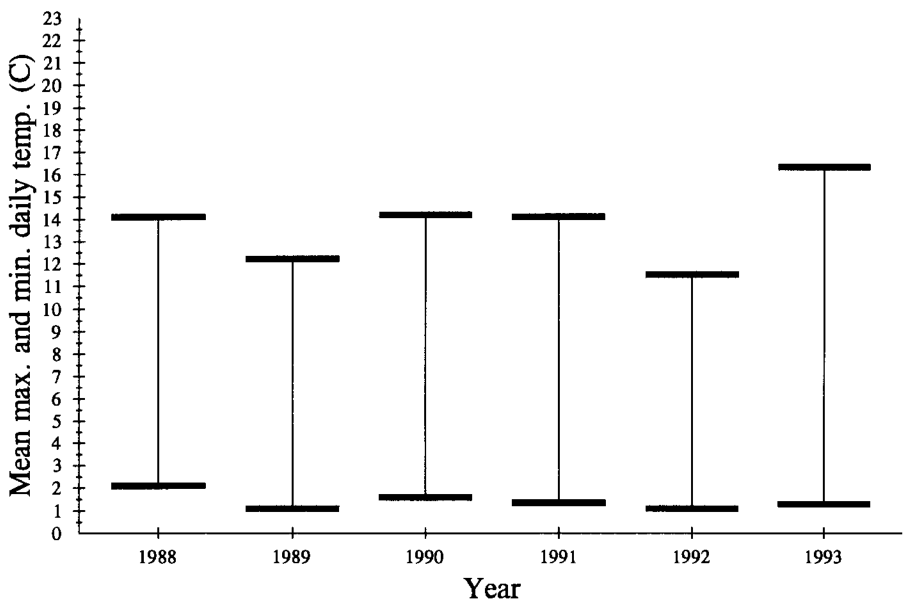


Figure 6. Annual mean maximum daily temperature and mean minimum daily temperature, Denali National Park, Alaska, 1988-1993. The top graph shows data collected from 15 March to 15 April; the bottom graph shows data collected from 16 April to 30 June. Mean maximum daily temperatures differed significantly among years during both periods ($H = 23.08$, $P = 0.003$ for top graph; $H = 47.21$ $P < 0.001$) for bottom graph). Mean minimum daily temperatures from 15 March to 15 April differed significantly among years ($H = 31.64$, $P = 0.002$).

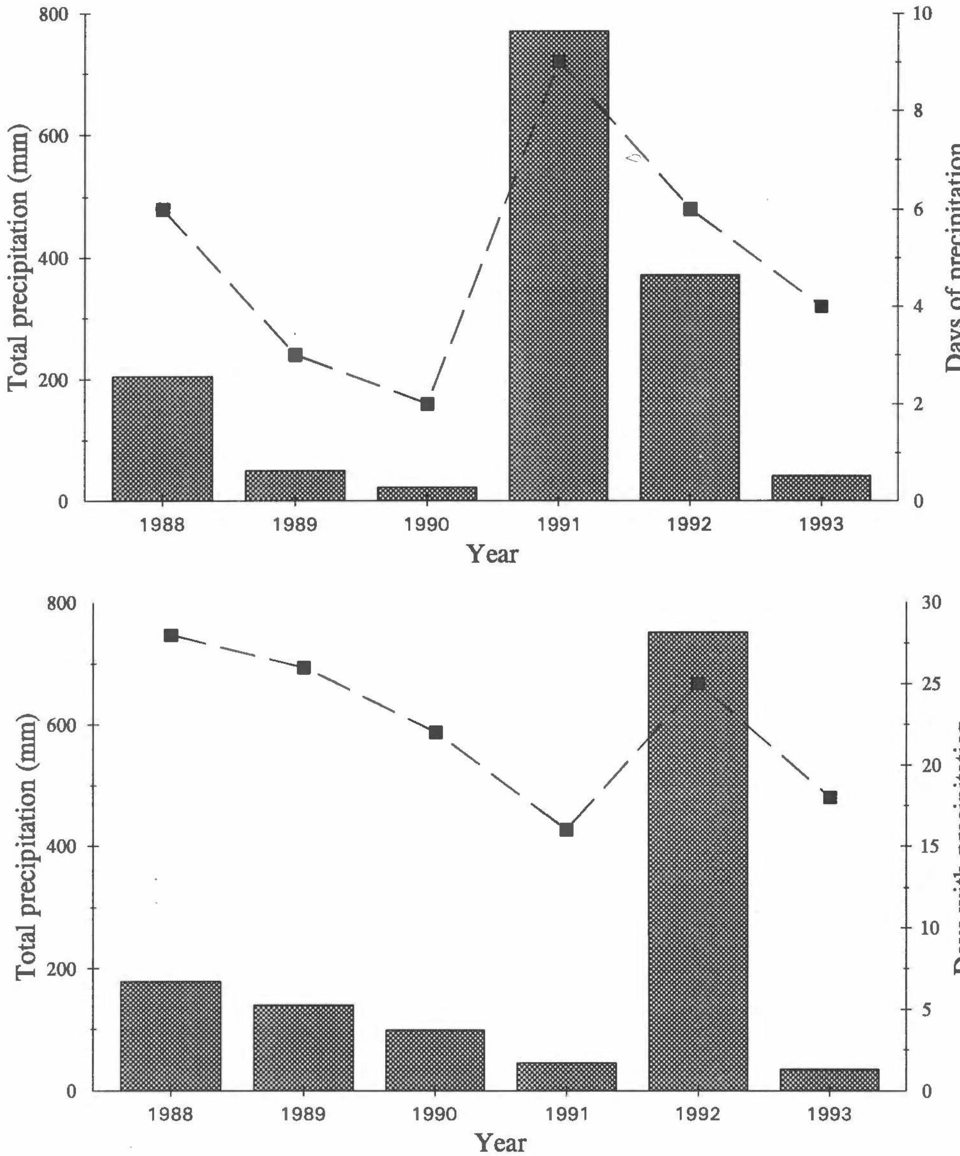


Figure 7. Total precipitation and days with precipitation, Denali National Park, Alaska, 1988-1993. The top graph shows data collected from 15 March to 15 April; the bottom graph shows data collected from 16 April to 30 June. Shaded-bars represent total precipitation. Dashed-lines with solid squares represent days with precipitation. Mean daily precipitation differed significantly among years during both periods (H = 22.51, P = 0.018 for top graph; H = 28.22, P = 0.003 for bottom graph).

Table 4. Spearman rank correlations between mean values of golden eagle reproductive variables and weather variables, Denali National Park, Alaska, 1988-1993. Pairs nesting examined against weather variables collected from 15 March - 15 April. Pairs successful and productivity examined against weather variables collected from 16 April-30 June.

	Weather Variable			
Reproductive component	Mean max. daily temp.	Mean min. daily temp.	Total precipitation	Precipitation days
Pairs nesting	0.142 NS	-0.542 NS	-0.257 NS	-0.492 NS
Pairs successful	-0.029 NS	0.147 NS	-0.202 NS	0.058 NS
Productivity	-0.142 NS	0.318 NS	0.286 NS	-0.549 NS

NS = not significant, $P \geq 0.05$

Patterns in nesting territory occupancy

Of the 74 nesting territories monitored during this study, 43 (58.1%) were occupied every year and six (8.1%) were unoccupied every year of the study (Appendix 1). Observed distribution of frequencies of occupation of nesting territories over the 6 years differed significantly from the pattern expected if territories were occupied at random (χ^2 =2,067.16, d.f. = 6, $P < 0.001$; Fig. 8). Forty-three nesting territories were occupied more often that expected, whereas 31 were occupied less frequently (Fig. 8). Nesting success and productivity were positively correlated with the number of years that a territory was occupied ($r_s = 0.34$, $P = 0.004$ for nesting success; $r_s = 0.36$, $P = 0.002$ for productivity; Fig. 9).

Nesting territories classified as presumed unoccupied ranged from one to six among years ($\bar{x} = 3.67$, S.D. = 2.07). If, indeed, these territories were occupied (e.g., I failed to detect a territorial pair), estimates of nesting-territory occupancy would be marginally higher and estimates of reproductive variables would be marginally lower that those presented in Table 1.

The number of territories where lone adults were observed ranged from one to zero among years. Because I did not detect a pair of eagles after repeated visits, these territories were considered unoccupied.

Patterns in reproduction among nesting territories

Territorial pairs did not lay eggs every year (Appendix 1). Only 13 (19.1%) of

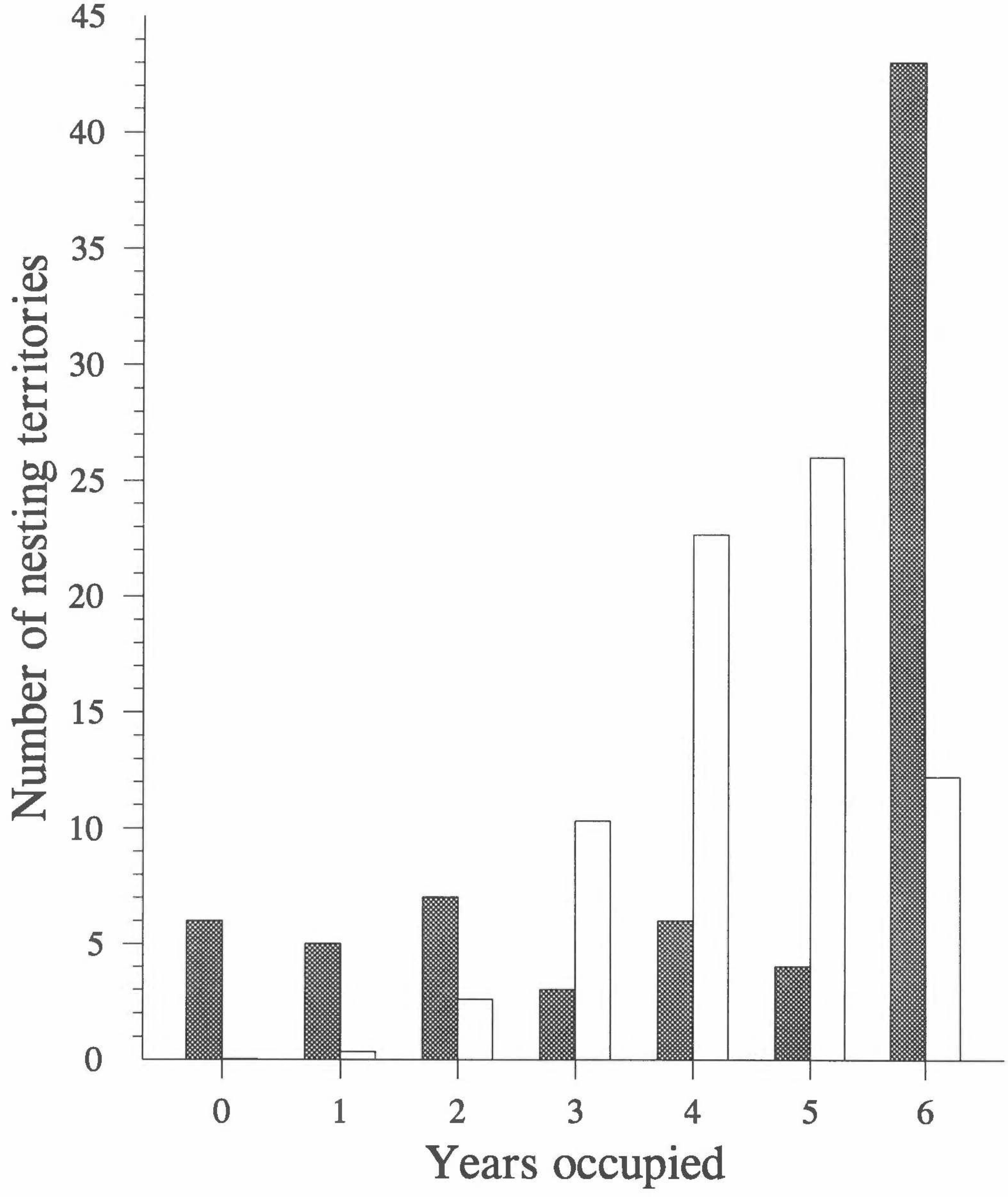


Figure 8. Frequency distribution of the number of years 74 golden eagle nesting territories were occupied, Denali National Park, Alaska, 1988-1993. Observed occupancy (shaded-bars) is compared with a random (Poisson) model (open-bars). The difference between observed and expected was significant ($\chi^2 = 2067.16$, d.f. = 6, $P < 0.001$).

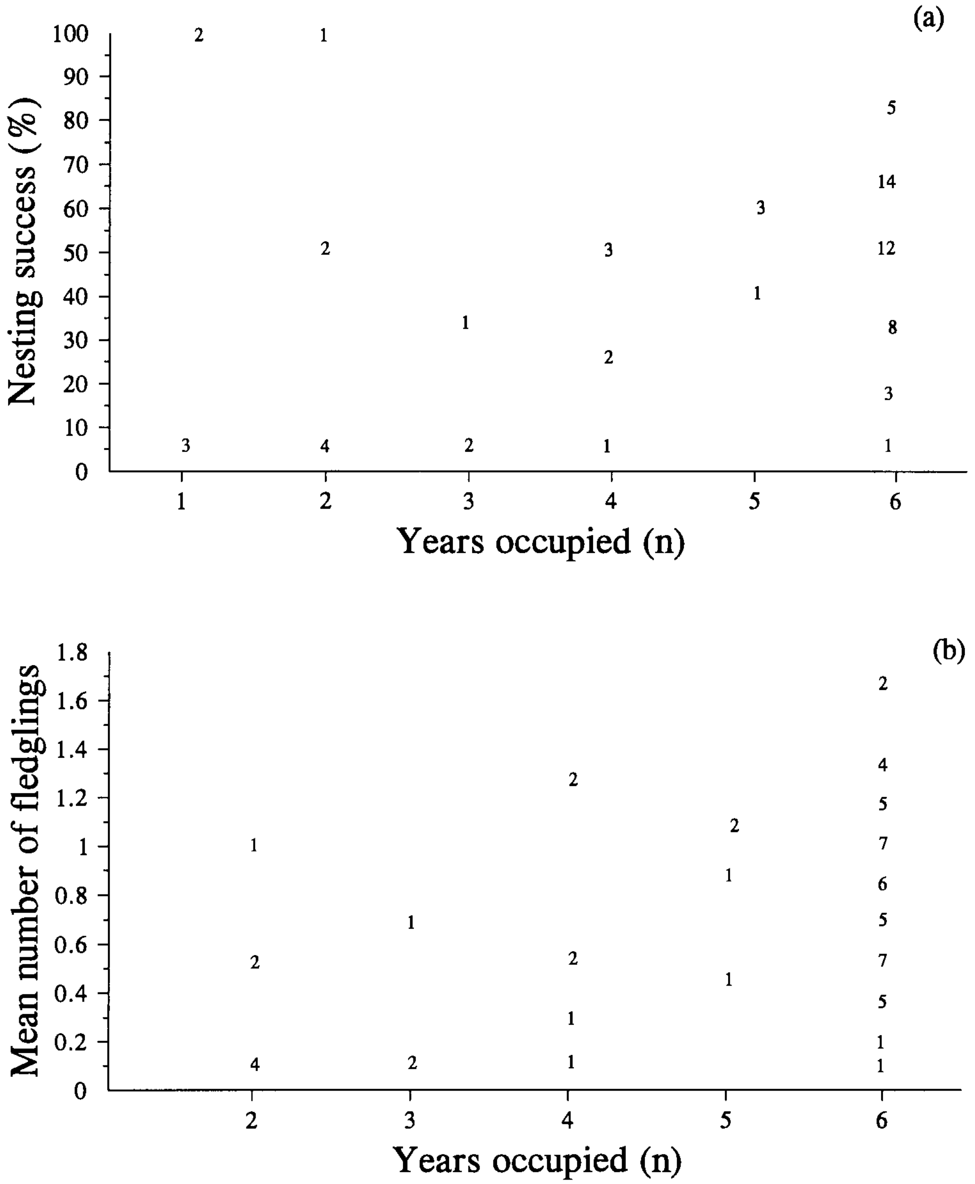


Figure 9. Correlations between occupancy of nesting territories and reproduction of golden eagles, Denali National Park, Alaska. Correlations between the number of years that nesting territories were occupied and: (a) nesting success ($r_s = 0.34$, $P = 0.002$, n = 68); and (b) productivity ($r_s = 0.38$, $P = 0.002$, n = 63). Data were collected over 6 connsecutive nesting seasons. Numbers in scatter plots represent number of nesting territories for each data point.

the 68 nesting territories occupied for more than 1 year contained nesting pairs in all years. Six of these territories (46.2%) were occupied every year, one (7.7%) was occupied only 4 years, one (7.7%) was occupied only 3 years, two (15.4%) were occupied only 2 years, and three (23.1%) were occupied only 1 year.

Productivity was higher at nesting territories occupied the longest (Fig. 9). Mean productivity greater than the 6-year mean of 0.78 was observed at 31 nesting territories. Of these, 24 (77.4%) were occupied for 6 years. Highest production observed during the study (10 fledglings), was recorded at 2 territories, both which were occupied for 6 years. Of 251 fledglings produced during this study, 242 (96.4%) were produced at nesting territories occupied $\geq$ 4 years (n = 52), with the greatest number of fledglings (n = 211) produced at nesting territories occupied all 6 years.

Comparison of reproduction among study areas

I compared reproduction of golden eagles in Denali with golden eagles from 14 geographically distinct areas (Table 5). Seven studies provided estimates of percentage of pairs nesting each year (range = 71 - 95%), of which Denali (71%) ranked lowest. Thirteen studies provided estimates of nesting success (range = 40 - 71%), of which Denali (50%) ranked tenth. Twelve studies provided estimates of mean number of fledglings produced per territorial pair (range = 0.54 - 0.99), of which Denali (0.78) ranked fifth. Finally, all studies provided estimates of number of fledglings produced per successful pair (range = 0.65 - 1.70), of which Denali (1.51) ranked third.

Table 5. Comparison of reproductive characteristics of golden eagles among geographically distinct areas.

Study area	Years of study	Pairs per year	% pairs nesting (range %)	% pairs successful (range %)	Fledglings/ territorial pair (range)	Fledglings/ successful pair (range)	Reference
Denali Park, Alaska	6	49-61	70 (36-87)	50 (28-65)	0.78 (0.36-1.12)	1.51 (1.33-1.71)	This study
Kilbuk Mts., western Alaska	4	11-13	95 (85-100)	67 (55-83)	0.99 (0.73-1.25)	1.49 (1.33-1.63)	McCaffery (unpubl. data)
Yukon, Canada	12	NA	NA	59 (35-90)	0.63 (0.35-0.90)	1.40 (1.00-1.60)	Mossop et al. (1986)
NW Territories, Canada	4	11-20	NA	49 (40-64)	0.63 (0.55-0.73)	1.29 (1.14-1.50)	Poole and Bromley (1988)
Kilbuk/ Ahklun Mts., Alaska	10	32-35	NA	44 (NA)	NA	1.70 (NA)	Petersen al. 1991
Porcupine River, Alaska	4	11-13	NA	NA	NA	1.50 (1.33-1.60)	Ritchie and Curatolo (1982)
Southwestern Idaho	22	28-35	80 (38-100)	61 (32-80)	0.81 (0.16-1.23)	1.56 (1.00-2.00)	Lehman et al. (1993)
Northeastern Wyoming	6	85-140	81 (38-100)	61 (32-80)	0.81 (0.52-1.16)	1.48 (1.33-1.65)	Phillips and Beske (1990)

NA = data not presented in original reference

Table 5. (Cont'd). Comparison of reproductive characteristics of golden eagles among geographically distinct areas.

Study area	Years	Pairs per year	% pairs nesting (range)	% pairs successful (range)	Fledglings/ territorial pair (range)	Fledglings/ successful pair (range)	Reference
Northeastern Scotland	13	5	86 (60-100)	71 (25-100)	0.80 (0.20-1.40)	1.40 (1.00-2.00)	Watson (1957)
Sweden	6	28-46	77 (36-100)	53 (21-85)	0.64 (0.27-1.24)	1.21 (1.00-1.46)	Tjernberg (1983a)
Northern Finland	7	>25	NA	NA	0.54 (NA)	1.31 (NA)	Sulkava et al. (1984)
Southwestern Norway	21	4-14	NA	40 (0-100)	0.58 (0-1.8)	1.28 (1.0-2.0)	Gjershaug (In press)
Swiss Alps, Switzerland	5	48	79 (NA[a])	62 (NA)	NA	0.65 (NA)	Haller (1982)
Appennines Mts., Italy	7	2-9	NA	57 (33-83)	0.58 (0.33-0.83)	1.00 (1.00-1.00)	Margrini et al. (1986)
Estonia, Russia	12	8-16	NA	52 (25-79)	0.56 (0.25-0.78)	1.08 (0.25-0.78)	Randla (1986)

DISCUSSION

Variation in reproduction

Productivity remained stable for the first 4 years of my study, but declined significantly in 1992 and 1993. The difference in productivity between the best year (1.12 fledglings per territorial pair) and the worst year (0.36 fledglings per territorial pair) was over threefold. Similar variation in productivity of golden eagles has been recorded elsewhere (Watson 1957, Tjernberg 1983a, Phillips and Beske 1990, Lehman et al. 1993). Fledgling production was greater in years when higher percentages of pairs nested. Percentage of pairs nesting was positively correlated with numbers of snowshoe hare and willow ptarmigan observed in the study area, suggesting that more pairs lay and more young are fledged when numbers of ptarmigan and hare are high.

Although I did not measure clutch size during this study, consistency in the mean number of fledglings produced per successful pair (Table 1) suggests little variation in clutch size. Other studies have shown that clutch sizes of golden eagles are constant among years (McGahan 1968, Reynolds 1969, Kochert 1972, Beecham and Kochert 1975). Variation in clutch size, therefore, probably is not an important factor influencing productivity in Denali.

The percentage of territorial pairs of golden eagles that did not lay eggs in a particular year in Denali ranged between 13.5 % and 63.5%. Nonbreeding also has been documented for other large eagles (Brown 1970, Sherrod et al. 1976, Swenson et al. 1986, Hustler and Howells 1987, Gerrard and Bortolotti 1988, Gargett 1990). Decreases in the percentage of pairs nesting coincided with observed decreases in both hare and ptarmigan in my study area. This suggests that some golden eagles in Denali adopted an "energetically conservative strategy of nonbreeding" (Collopy 1980) when food supplies on the breeding grounds were low. My findings are consistent with those of Gargett (1990), Brown (1976), Dennis et al. (1984), Petersen et al. (1991), and Watson et al. (1992), reported increasing rates of nonbreeding in large eagles when food supplies decreased.

Many instances of correlations between food supplies and reproduction have been documented in birds (e.g., Lack 1966, King 1973, Newton 1980, Arcese and Smith 1988, Mossop and Hayes 1994). Newton (1979) reviewed substantial evidence that much natural variation in reproductive success of raptors can be explained ultimately by variation in their food supply. Additionally, avian predators that depend primarily upon cyclic populations of prey (e.g., hare and ptarmigan) often adjust their reproduction in response to prey abundance (Pitelka et al. 1955, Galushin 1974, Nielsen and Cade 1990, Mossop and Hayes 1994). Many other investigators reported that prey availability or prey abundance are major factors regulating reproduction in golden eagles (Tjernberg 1983a, K. Steenhof and M. Kochert, pers. comm., Phillips and Beske 1990, Lehman et al. 1993, Watson et al. 1992). For example, in arid parts of the western United States the reproductive success of golden eagles varies with the abundance of black-tailed jackrabbits (Murphy 1975, Beecham and Kochert 1975). Good years of reproductive success in golden eagles in Scotland often coincides with periods of high numbers of red grouse (*L. lagopus scoticus*) or hare (*L. timidus*) (Newton 1979). Swartz et al. (1975) suggested that a relationship occurs between nesting golden eagles and ptarmigan numbers on the Seward Peninsula in western Alaska. Based on my results, I predict that proportions of golden eagles laying in Denali will increase when numbers of hare and ptarmigan increase in the study area.

Nesting success and productivity were not correlated with numbers of hare and ptarmigan. Golden eagles return to their nesting territories in Denali at a time when the diversity and abundance of prey are low, and hare and ptarmigan are two of the most common prey species available. As other prey species (e.g., arctic ground squirrel, hoary marmot, and microtenes) become available as the nesting season progress, the importance of hare and ptarmigan as food sources for golden eagles may decrease.

The annual rate (%) of territorial pairs nesting in Denali was the lowest compared with six other populations of golden eagles. I propose several reasons why lower nesting rates were recorded in Denali compared with other studies. First, costs of reproduction may be greater for migratory golden eagles than for golden eagles that remain on their nesting territories throughout the year. Golden eagles in other study areas are residents; golden eagles in Denali are migratory. Second, greater fluctuations in food supply may occur in study areas in subarctic areas compared with study areas in temperate regions. Third, the diversity of prey available before nesting may be lower in Arctic and subarctic areas than in temperate areas and golden eagles in temperate areas may have more species available as food before laying begins than golden eagles in subarctic areas. No studies to date, however, have investigated this aspect of golden eagle ecology, and no data are available to test any of these hypotheses.

Population stability

Little quantitative information is available on numbers and reproduction of golden eagles in Denali before 1987. Sheldon (1930) mentioned that golden eagles were "common" in this area in the early 1900's. Dixon (1938) reported that golden eagles were "widely distributed and relatively abundant" in this area during the 1920's and 1930's. Murie (1944) estimated that at least 25 pairs of golden eagles were nesting in the area referred to as the "Sheep Hills," which composes about 75% of my study area. Although no historical data are available to detect changes in size or to compare reproductive characteristics of the local breeding population of golden eagles, it appears that golden eagles have been a common breeding species in Denali since at least the early 1900's.

During my study, occupancy of nesting territories was high and did not vary significantly among years. My findings are similar to results from other long-term studies on stable populations of golden eagles (Brown and Watson 1964, Haller 1982, Phillips et al. 1984, Phillips et al. 1990), suggesting that the breeding population of golden eagles in Denali is stable.

Not all nesting territories in my study area were occupied by golden eagles every year and six nesting territories were never used by eagles during the 6-year study. Although I did not address causes of variation in occupancy of nesting territories, occupancy may be related to physical characteristics of territories or proximity to a dependable prey base (Newton 1979). Lack of use of some nesting territories could be caused by a shortage of potential breeders or may suggest that these territories are of poorer quality compared with others. Continuous occupation of some nesting territories suggests that these nesting territories maybe more "attractive" or of "higher" quality than those occupied occasionally (Newton 1986, Gargett 1990, Birkhead 1991).

Golden eagles are long-lived with strong fidelity to nesting territories (Newton 1979, Cramp and Simmons 1980, Palmer 1988). Nesting in the same territory year after year should be advantageous for golden eagles if they are on good territories (Newton 1979). Although I could not identify individual golden eagles, given their strong fidelity to nesting areas, many of the same pairs probably occupied the same nesting territories in consecutive years during my study.

Because demographic data (e.g., recruitment and survivorship) are not available, I could not assess recruitment necessary for population stability of golden eagles in Denali. The 6-year average of 0.78 fledglings per territorial pair in Denali, however, is comparable to the mean productivity of golden eagles in other study areas (range = 0.54-0.99) where territorial numbers have remained stable. Reproduction at nesting territories showing the lowest productivity (means of 0-0.40 fledglings per year) seems inadequate for population stability (following Phillips et al. 1990).

Nesting phenology

Estimates of nesting phenology reported in this paper are biased toward successful nests because hatch dates were calculated from nestlings only at successful nests. My estimates, however, provide contemporary baseline information on the timing of golden eagle nesting events in interior Alaska. For instance, Murie (1944) reported that golden eagle eggs in Denali generally hatch in June, often in the later part of that month. My estimates of hatching dates are nearly a month earlier than those made by Murie (1944), but are similar to those reported by Ritchie and Curatolo (1982) along the Porcupine River, Alaska, by Mossop et al. (1986) in the southern Yukon Territory, Canada, by Poole and Bromley (1988) in the central Canadian Arctic, Northwest Territories, Canada, by Peterson et al. (1991) in the Kilbuk and Ahklun Mountain region, Alaska, and by Young et al. (1995) in the northeastern Brooks Range in Alaska.

Golden eagles have a nesting period (incubation and nestling period) of approximately 115 days (Palmer 1988). In northern areas, laying must occur early enough to provide time for newly fledged birds to gain flying and hunting skills before autumn migration. In Denali, for instance, eagles hatched in early June will fledge in early August, about 6 weeks before initiation of autumn migration.

The transition period from fledging to independence in young eagles has not been well-studied (Brown 1966, Kussman 1977, Alonso et al. 1987, Gargett 1990, Bahat 1992). Bahat (1992) reported that golden eagle fledglings depended largely on their parents for food during the first 68 days following fledging. Satellite telemetry studies on fledgling golden eagles in Denali suggest that autumn migration begins in late September (McIntyre et al. 1991). If the post-fledgling period in Denali is similar to that recorded by Bahat (1992), golden eagle fledglings will rely on their parents for food after the initiation of migration. Bahat (1992) also reported that flight distance, flight duration and flight performance of fledged golden eagles increased with age. Laying early, therefore, would be advantageous for golden eagles nesting in northern areas to maximize the post-fledging period before migration begins.

Enhanced nesting success and productivity associated with early nest initiation have been observed in sparrowhawks (*Accipiter nisus*) (Newton 1986), peregrine falcons (*Falco peregrinus*) (Mearns and Newton 1988), Eurasian kestrels (*F. tinnunculus*) (Village 1990), and several other species of raptors (Newton 1979). I could not determine the influence of nesting phenology on nesting success because laying dates for all nesting pairs were unknown. Hatch date did not appear to influence brood size for successful nests; broods that hatched earlier were not larger than broods that hatched later.

Weather and reproduction

Newton (1979) suggested that variation in weather acts on reproduction in raptors mainly by influencing prey availability, hunting efficiency or food needs, and sometimes causing death in extreme conditions. I failed to detect any relationships between weather variables and reproduction during this study.

The literature contains contrasting views on the influence of weather on reproduction in golden eagles. In Scotland breeding of eagles in spring is little, if at all, influenced by weather in the preceding winter Watson (1957). In Idaho, however, severe weather in winter negatively affected reproduction by golden eagles in years when the food supply was low (Lehman et al. 1993). Additionally, cold temperatures in winter were associated with reduced numbers of eagle pairs laying in Idaho (K. Steenhof and M.N. Kochert, pers. comm.) and poor weather in spring depressed the breeding success of golden eagles in France (Clouet 1981). In Sweden, unusually favorable weather could explain unexpectedly good breeding success in golden eagles in a year when prey was scarce (Tjernberg1983a). Weather also has affected nesting success by destroying nesting structures or directly killing nestlings (Beecham and Kochert 1975, Watson et al. 1987, Phillips et al. 1990).

In Denali, weather may affect individual pairs of eagles differently; however, these effects may be difficult to detect when measurements are made at the population level. Although weather also may act indirectly on eagles by influencing prey availability or abundance (Newton 1979), no data are currently available to examine relationships between prey abundance or prey availability and weather in Denali.

Patterns of reproduction within nesting territories

Temporal variation in factors such as food supply may contribute to annual variation in reproduction in raptors (Newton 1979). Accordingly, some nesting territories in Denali may support breeding pairs of golden eagles only in favorable years (e.g., years when food supply is good). The poorest production during my study occurred in 1992. Of the 15 territories where fledglings were produced in 1992, 12 (80%) were occupied every year of my study and 10 (67%) had mean annual productivity $\geq$ 1.00 among years. Because pairs in these territories were successful during the poorest year, were these the "best" nesting territories during my study? Did these territories contain the "highest quality" birds during 1992? Was nesting success influenced by a combination of factors and will reproduction at these territories change when mortality and turnover occur in the population? Unfortunately, these questions cannot be addressed until further studies are conducted on quality of nesting territories and techniques are developed to identify individual eagles within nesting territories.

CONCLUSIONS AND RECOMMENDATIONS

My results show that: (1) a large, stable population of golden eagles breeds in the northeastern portion of Denali; (2) golden eagles in Denali had lower nesting rates than golden eagles in other study areas, but reproductive rates comparable to golden eagles at lower latitudes; (3) fewer pairs laid eggs when willow ptarmigan and snowshoe hare numbers were low; (4) nesting success and productivity decreased when the proportion of pairs nesting decreased; (5) more fledglings were produced at certain nesting territories than others; (6) overall, the best production occurred at territories occupied most consistently; (7) weather variables did not significantly influence reproduction; and (8) nesting phenology in Denali is similar to that of golden eagles in other study areas in Alaska and western Canada.

My study provides contemporary baseline data on occupancy of nesting territories and reproduction of golden eagles in Denali, however many other aspects of golden eagle ecology require future study. I offer the following observations and recommendations for future research on golden eagles in Denali and other northern study areas.

First, baseline data on populations are needed for all species used as prey by golden eagles to assess the effect of food supply on reproduction in golden eagles. Although I detected a relationship between the percentage of pairs nesting and hare and ptarmigan numbers, no data are available to assess the relationship of golden eagle reproduction with other foods (e.g., arctic ground squirrel, hoary marmot and microtenes) of these raptors. Additional research is needed to determine the importance of different prey species in diets of golden eagles throughout the nesting season. Other research is needed to determine how changes in numbers of one prey species affect other prey species and if cycles of willow ptarmigan and snowshoe hare occur simultaneously.

Second, does food supply on the wintering grounds affect reproduction of golden eagles on the breeding grounds? Because golden eagles that breed in Denali spend the winter away from the breeding grounds, determining the influence of the wintering range on reproduction is important.

Third, estimates of longevity, survivorship, recruitment and lifetime reproductive success of golden eagles are needed for a more thorough understanding of the species throughout its range. Are survival rates of migratory golden eagles different from resident golden eagles? Is recruitment different at higher latitudes than temperate areas? Research on obtaining estimates of survivorship and turnover rates of golden eagles in Denali using molecular genetic techniques is pending (K. Scribner, pers. comm.). Other demographic data, (e.g., juvenile mortality rates and recruitment rates) will be difficult to obtain due to difficulties in catching and marking eagles, following marked eagles from fledgling to recruitment, and collecting data over many years on marked individuals.

Fourth, post-fledging periods for eagles in Denali should be determined and assessed in terms of long-term survival. Are post-fledging periods in Denali similar to other study areas and how long do juveniles rely on their parents for food? Do juvenile golden eagles from Denali begin migration with their parents, how long do family groups remain together and does this influence future survival of adults and offspring? Are mortality rates of juvenile golden eagles higher in migratory populations? How do these factors influence long-term stability of golden eagle populations in northern latitudes?

Fifth, do nesting territories differ in their physical characteristics? Can nesting territories be rated as good or poor based on physical characteristics and how does territory quality influence occupancy and reproduction? Do physical characteristics of territories differ significantly among years and how does this influence occupancy of areas and reproduction in those areas?

Finally, migratory routes and wintering areas of Denali's golden eagles should be determined using satellite telemetry to identify and assess potential threats to golden eagles. Subsequently, research should address the influence of wintering-range conditions on reproduction in golden eagles. Locating migration routes and wintering areas of golden eagles from Denali using banding data alone can be painfully slow. For instance, nearly 200 nestlings were banded in Denali from 1987-1993, but only four have been recovered to date. In 1990 and 1992, however, I used satellite radio telemetry to track juvenile golden eagles from Denali to their respective wintering locations (McIntyre et al. 1991, McIntyre, unpublished data). Satellite telemetry provided instantaneous information on the location of the radio-tagged eagles throughout autumn migration and most of the wintering period. Recent advances in satellite technology allow for long-term tracking of eagles (> three years) which will provide data on migration routes, wintering areas, and summer distribution.

At this time, the population of golden eagles in Denali appears stable. Reasons for changes in this population, however, will be speculative until other aspects of the ecology (e.g., food supply, demographics, habitat, and wintering locations) of golden eagles are studied.

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Appendix 1. Comprehensive summary of occupancy and reproduction measured at 68 golden eagle nesting territories for six consecutive breeding seasons, Denali National Park, Alaska, 1988-1993.

Terr. ID #	No. of years occupied (%)	Years with nesting pairs (%)	Years with successful nests (%)	Reproductive pattern[a]	Total no. fledglings produced	Mean no. fledglings/ occ. year
2	6 (100)	6 (100)	5 (83)	S-S-S-F-S-S	8	1.33
3	6 (100)	4 (67)	4 (83)	S-S-S-O-S-O	6	1
6	6 (100)	6 (100)	4 (67)	F-S-S-S-F-S	4	0.67
7	5 (83)	3 (60)	3 (60)	S-G-S-O-S-O	5	1
8	6 (100)	6 (100)	3 (50)	S-S-F-S-F-F	3	0.5
9	6 (100)	5 (83)	3 (50)	F-S-O-S-F-S	3	0.5
10	5 (83)	3 (60)	2 (40)	O-G-S-O-F-S	2	0.4
11	6 (100)	2 (33)	2 (33)	O-S-O-S-O-O	2	0.33
12	6 (100)	4 (67)	2 (33)	S-O-S-S-O-F	3	0.5
13	2 (33)	2 (100)	2 (100)	S-S-L-G-G-U	2	1
14	6 (100)	5 (83)	5 (83)	S-S-S-S-O-S	10	1.67
16	6 (100)	6 (100)	4 (67)	S-S-S-S-F-F	5	0.83
17	6 (100)	5 (83)	4 (67)	S-S-S-O-S-F	10	1.67
18	6 (100)	5 (83)	4 (67)	S-O-S-S-F-S	6	1
19	6 (100)	5 (83)	3 (50)	S-F-F-S-S-O	6	1
21	4 (67)	4 (100)	2 (50)	F-?-?-S-F-S	2	0.5
22	6 (100)	3 (50)	3 (50)	O-S-O-S-S-O	3	0.5
23	6 (100)	3 (50)	0	O-F-O-F-F-O	0	----
26	1 (17)	1 (100)	1 (100)	U-U-U-S-L-U	1	1.00

[a] legend to reproductive pattern symbols: **S** = successful nesting attempt, **F** = failed nesting attempt, **O** = occupied by a pair but no nesting (nonbreeding year), **U** = territory unoccupied, **?** = occupancy of territory could not be determined, **G** = territory occupied by gyrfalcons.

Appendix 1 (cont'd). Comprehensive summary of occupancy and reproduction measured at 68 golden eagle nesting territories for six consecutive breeding seasons, Denali National Park, Alaska, 1988-1993.

Terr. ID #	No. of years occupied (%)	Years with nesting pairs (%)	Years with successful nests (%)	Reproductive pattern[a]	Total no. fledglings produced	Mean no. fledglings/ occ. year
27	1 (17)	1 (100)	0	F-?-L-L-L-L	0	----
28	5 (83)	3 (60)	3 (60)	S-G-O-S-S-O	5	1
29	6 (100)	3 (50)	2 (33)	S-O-F-O-S-O	2	0.33
30	5 (83)	3 (60)	3 (60)	S-S-?-S-O-O	4	0.8
31	6 (100)	5 (83)	5 (83)	S-S-S-S-S-O	6	1
32	4 (67)	3 (75)	1 (25)	S-F-G-U-F-O	1	0.25
33	2 (33)	2 (100)	1 (50)	S-F-U-U-U-L	1	0.25
34	2 (33)	1 (50)	0	F-O-U-U-U-U	0	----
35	6 (100)	5 (83)	4 (66)	S-S-S-O-F-S	6	1
36	6 (100)	6 (100)	3 (50)	F-F-S-S-F-S	3	0.5
37	6 (100)	4 (67)	4 (67)	S-S-S-O-S-O	7	1.16
38	6 (100)	5 (83)	4 (66)	S-S-S-S-F-O	7	1.16
39	6 (100)	5 (83)	4 (67)	S-S-F-S-S-O	8	1.33
40	6 (100)	4 (67)	3 (50)	S-S-F-O-O-S	5	0.83
41	6 (100)	2 (33)	2 (33)	O-O-S-S-O-O	4	0.67
42	6 (100)	4 (67)	4 (66)	0-S-S-S-S-O	7	1.16
44	1 (17)	0	0	?-U-U-U-R-O	0	----
45	3 (50)	2 (67)	0	G-F-G-G-F-O	0	----

[a] legend to reproductive pattern symbols: **S** = successful nesting attempt, **F** = failed nesting attempt, **O** = occupied by a pair but no nesting (nonbreeding year), **U** = territory unoccupied, **?** = occupancy of territory could not be determined, **G** = territory occupied by gyrfalcons.

Appendix 1 (cont'd). Comprehensive summary of occupancy and reproduction measured at 68 golden eagle nesting territories for six consecutive breeding seasons, Denali National Park, Alaska, 1988-1993.

Terr. ID #	No. of years occupied (%)	Years with nesting pairs (%)	Years with successful nests (%)	Reproductive pattern[a]	Total no. fledglings produced	Mean no. fledglings/ occ. year
46	6 (100)	5 (83)	3 (50)	F-S-S-F-O-S	4	0.67
47	6 (100)	3 (50)	3 (50)	S-S-O-O-O-S	5	0.83
48	6 (100)	5 (83)	3 (50)	F-S-S-S-O-F	6	1
49	6 (100)	4 (67)	2 (33)	S-S-F-O-S-O	5	0.83
50	6 (100)	5 (83)	5 (83)	S-S-S-S-O-S	7	1.16
51	6 (100)	3 (50)	1 (17)	O-F-S-F-O-O	1	0.17
55	6 (100)	2 (33)	1 (17)	O-S-F-O-O-O	2	0.33
58	6 (100)	4 (67)	4 (67)	S-S-S-S-O-O	6	1
64	2 (33)	0	0	U-U-U-U-O-O	0	----
66	4 (67)	1 (25)	1 (25)	F-U-U-S-O-O	2	0.5
67	2 (33)	1 (50)	0	L-?-?-G-F-O	0	----
69	6 (100)	4 (67)	3 (50)	S-S-S-O-O-F	3	0.5
70	2 (33)	1 (50)	0	?-?-F-U-L-O	0	----
72	6 (100)	4 (67)	1 (17)	O-F-F-F-O-S	2	0.33
75	6 (100)	4 (67)	4 (67)	O-S-S-S-O-S	7	1.16
76	6 (100)	2 (33)	2 (33)	O-S-O-S-O-O	3	0.5
77	6 (100)	6 (100)	5 (83)	S-S-S-S-F-S	8	1.33
78	1 (17)	1 (100)	1 (100)	S-G-G-G-G-G	2	2
79	6 (100)	5 (83)	2 (33)	S-F-S-O-F-F	2	0.33

[a] legend to reproductive pattern symbols: **S** = successful nesting attempt, **F** = failed nesting attempt, **O** = occupied by a pair but no nesting (nonbreeding year), **U** = territory unoccupied, **?** = occupancy of territory could not be determined, **G** = territory occupied by gyrfalcons.

Appendix 1 (cont'd). Comprehensive summary of occupancy and reproduction measured at 68 golden eagle nesting territories for six consecutive breeding seasons, Denali National Park, Alaska, 1988-1993.

Terr. ID #	No. of years occupied (%)	Years with nesting pairs (%)	Years with successful nests (%)	Reproductive pattern[a]	Total no. fledglings produced	Mean no. fledglings/ occ. year
80	1 (17)	0	0	O-?-?-?-?-?	0	----
81	6 (100)	2 (33)	2 (33)	O-S-O-S-O-O	4	0.67
82	6 (100)	5 (83)	3 (50)	F-F-S-S-S-O	4	0.67
83	6 (100)	4 (67)	4 (67)	S-S-F-S-F-S	8	1.33
84	6 (100)	5 (83)	4 (67)	S-S-S-S-F-O	5	0.83
85	4 (67)	1 (25)	0	O-O-G-F-O-G	0	----
86	4 (67)	2 (50)	2 (50)	S-?-O-S-L-O	5	1.25
95	3 (50)	2 (67)	0	F-?-?-?-O-F	0	----
96	4 (67)	3 (75)	2 (50)	S-S-F-G-?-O	5	1.25
97	6 (100)	4 (83)	3 (50)	S-O-S-S-O-F	5	0.83
101	3 (50)	3 (100)	1 (33)	S-F-G-G-?-F	2	0.67
108	2 (33)	1 (50)	1 (50)	U-U-U-U-S-O	1	0.5

[a] legend to reproductive pattern symbols: **S** = successful nesting attempt, **F** = failed nesting attempt, **O** = occupied by a pair but no nesting (nonbreeding year), **U** = territory unoccupied, **?** = occupancy of territory could not be determined, **G** = territory occupied by gyrfalcons.